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Impact of early crop management on plant productivity in irrigated rice :

can plant plasticity compensate for different imposed tillering dynamics ?

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SOMMAIRE

INTRODUCTION

In small farms of Asia, rice seedlings are usually transplanted manually in the field. Transplanting plants in the field, after seedlings' emergence in a nursery, is the most used method in irrigated rice under high level of inputs. It is a good mean to eliminate weeds because of the water brought before transplanting which engenders a bad environment for weeds' emergence, and to obtain a homogeneous population since seedlings of same size are disposed in hills (word used to name each location in the field where seedlings are transplanted) of equivalent size with a regular spacing. Wet-bed nurseries are usually used by farmers to prepare rice seedlings for manual transplanting. Seedlings can be transplanted at 20 or 40 DAS.

Rice varieties, especially irrigated rice cultivated under high level of inputs, have a high tillering ability. On the one hand, tillering plays an important role in determining rice yield since it can have a significant influence on the future production of panicles (Miller *et al.*, 1991), which in turn is highly correlated with grain yield (Counce and Wells, 1990; Miller *et al.*, 1991). Too few tillers result in too few panicles; but excess tillers cause also high tiller abortion, small panicles, poor grain filling and a consequent reduction in grain yield (Peng *et al.*, 1994). Thus, Lafarge *et al.* (2002) showed that yield in sorghum canopy was affected by 20 % by the increase in plants density from 8 to 16 plants per square meter because of the higher senescence at the highest density. On the other hand, rice plant, thanks to its morphological plasticity, is able to compensate the initial contrasted conditions as nursery type or plant density after transplanting, thanks to a tiller production adapted to each environment and different in each case (Dingkuhn, 1996). In most cereals, grain yield is very stable over a wide range of plant densities as the tillering dynamics of the plants respond to the level of resources available (Seetharama *et al.*, 1984). Hence, crop management improvement in irrigated rice for an increase in yields needs a better control of tillering dynamic in order to decrease tiller senescence and to increase fertile tillers' productivity. The objectives of this study were to analyse in details the effects of different early crop managements on plant's behaviour in order to characterize tillering dynamics and in order to try to identify the factors controlling tillering and favourable to a better assimilates distribution within the plant, resulting in a better productivity.

The first tillers to appear are generally the most productive ones (Lafarge *et al.*, 2002; Lauer and Simmons, 1985). To see the contributions of the tillers to grain yield, a first general analysis of tillering dynamic was made. The first tillers which were supposed to contribute the most to grain yield were also removed in order to see if plant plasticity was able to compensate the presumed lost. Dingkuhn *et al.* (1987) observed that delaying plant's age at transplanting resulted in a tillering reduced, a lower percentage of senescent tillers and a greater yield. Schnier *et al.* (1990) showed that a high plant density engendered an earlier maximum tillering and a number of tillers per plant lower. The study analysed the effects of these kinds of early crop managements in other given conditions. Finally, we tried to find stable functions that explained tillering dynamic and ways to improve yield.

To analyse the effects of the removal of the first tillers to appear, of the delay in transplanting date and of the increase in density, a single variety (IR72) and a single type of nursery (wet-bed) corresponding to general practices were used. A reference treatment was established where first tillers remained intact, plants were transplanted at 7 DAS and at 25 plants m^{-2}. In the other treatments, first tillers were removed or plants were transplanted at 21 DAS or at a density of 50 plants m^{-2}.

1- MATERIALS AND METHODS

1.1. Plant material and growing conditions

An improved inbred line of rice (IR 72) was grown under optimal water, nutrient and weed management in a field experiment in IRRI, Los Banos (14 DG 11 MIN N, 121 DG 15 MIN E, 21 m a.s.l), Laguna, Philippines during the wet season. The soil texture was 64 % Clay, 29 % Silt and 7 % Sand, pH varied in the range from 6.4 to 7, the ECE (Electrical conductivity) was 1 $dS.m^{-1}$ and the CEC (Cation Exchange Capacity) 40-50 meq 100 g^{-1}. A randomized complete block design with a comparison of the treatments 2 by 2 was established : it consisted of two planting densities (25 and 50 plants m^{-2}), two transplanting dates (7 and 21 days after sowing - DAS) and two tillering treatments (primary tillers 2, 3 and 4 either removed as soon as they appeared or remained intact; see tillers' description below) in 4 replicates. The experiment was composed of the following four treatments:

1. WB 07-25-NR, transplanting date 7 DAS, density 25 plants m^{-2}, no tiller removal.
2. WB 07-25-TR, transplanting date 7 DAS, plant density 25 plants m^{-2}, tiller removal.
3. WB 21-25-NR, transplanting date 21 DAS, plant density 25 plants m^{-2}, no tiller removal.
4. WB 21-50-NR, transplanting date 21 DAS, plant density 50 plants m^{-2}, no tiller removal.

Seeds were soaked for 24 hours, drained and incubated for another 24 hours in order to promote germination. Pre-germinated seeds were sown at a rate of 3000 seeds m^{-2} in wet-bed nurseries (WB) close to the main field in IRRI farm. Wet-bed nurseries consist of strips of 1 to 1.5 cm wide and raised 4 to 5 cm above the original soil level to facilitate drainage. First, field was flooded, soil plowed, well puddled and water was maintained at a sufficient level to cover the soil and used as a guide to level the field. Sown seeds were recovered with a thin layer of soil. Seedbeds were watered 2 to 3 DAS and a water depth of 2 cm was maintained later on. After 7 or 21 DAS depending on the treatment, seedlings were pulled out from the nursery and manually transplanted in the main field. The field was previously flooded to realign soil particles in a manner that will reduce the water penetration and leave the surface level for crop establishment and carefully leveled 1 day before transplanting. Plots concerning treatment 1 were 5 m long and 3.5 m wide, treatment 2 was 5 m long and 3.5 m wide. 1 seedling was transplanted per hill which were separated from 20 cm between rows, and 20 cm in one row for treatments 1 to 3, 10 cm in one row for treatment 4. The usual practice would be to transplant 3 to 4 seedlings per hill, only one seedling was transplanted here to detect the effect of the treatment on a per plant basis. Water was provided by irrigation canals. Water depth was continuously maintained between 3 to 5 cm all over the growing period.

In all plots, nitrogen as 70 kg N ha^{-1} in the form of urea was applied before transplanting (basal), at mid-tillering and panicle initiation in three splits of 40, 20 and 10 kg N ha^{-1} respectively. In all plots, phosphorus (50 kg ha^{-1} as solophos), potassium (50 kg ha^{-1} as muriate of potash) and zinc (5 kg ha^{-1} as zinc sulphate). Molluscide was sprayed at 2, 8 and 15 DAS, Sofit (herbicide) at 15 DAS and handweeding was realised at 58 DAS. Insecticides as Furadan 3G was applied at 17, 38 DAS, as dimothrin and cymbush at 24 and 45 DAS, as cymbush only at 31 DAS and as Regent at 66 DAS. During the last three weeks before harvest, birdboys were looking after the field to avoid grain loss because of birds. A plastic enclosure was fixed around the field to keep the rats away. Plant nitrogen was never deficient during the experiment. In all treatments, leaf N dry weight varied from 4.5 to 5.5 % of the plant shoot dry weight between 7 and 21 DAS, from 5 to 5.5 % at 27 DAS and from 2-3.6 between 48 and 62 DAS. The critical level for deficiency for N is 2.5 % until PI and 2 % until flowering (Dobermann and Fairhurst, 2000). Grain N dry weight at maturity varied from 1.2 and 1.4 % of the plant shoot dry weight. Tissue N was determined by the Kjeldahl method (Bremner, 1965).

1.2. Climatic measurements

Measurements were obtained thanks to a meteorological station in IRRI. Daily temperature during the plant cycle (data from June 1 to September 30) had a minimum temperature average of 24.5 ºC and a maximum average of 31.5 ºC. Mean temperature was 28 ºC. It was similar with the temperatures observed during the period 1979-2002 (min.=24.2ºC, max.=31.4ºC, mean=28ºC). The radiation and the relative humidity (17.9 MJ/m^2 and 86.3% respectively) were slightly higher between June and September 2003 than during the past twenty years (16.7 MJ/m^2 and 84 %).

1.3. Measurement time frame

Seeds were sown on June 10, 2003. Measurements began at 7 DAS on June 17 in the nursery on 3 sets of 12 seedlings each and were taken twice a week. Specific dates were on June 17, 20, 24, 27 and July 1. Plants of treatment 1 were taken from the field while those of treatments 2 and 3 from the nursery. From 21 DAS on July 4 until August 7, measurements were taken weekly in each plot of the field. Measurements on treatment 2 began on July 4 one week after tiller removal. Measurements ended after maximum tillering had been reached, on August 14 for treatments 1 and 2 and August 18 for treatments 3 and 4.

1.4. Phenological measurements and calculations

Each leaf of the main tiller and each primary tiller of the plant were tagged in 11 groups of 4 hills per plot. The production of fully expanded leaves on the main tiller was recorded by noting leaf ligule appearance until ligule appearance of the final leaf. The mean of the values gave the total number of fully expanded leaves of the main tiller for each plot and measurement date. Leaves were numbered with rings of different colors from June 26 in treatments 1 and 2 and from July 15 in treatments 3 and 4. The first leaf had its leaf blade extremely small and was called “incomplete leaf”. As a consequence, the first leaf to appear was counted as leaf number two. The number of dead leaves was recorded in each plot for the main tiller of the tagged plants until flag leaf appearance. A leaf was considered dead if 50 % or less of its surface was green.

Tiller emergence was also observed on the tagged plants. The origin of each emerged primary tiller defined by the main tiller node from which it developed was marked by a ring of the same color as the ring of the leaf from which it emerged. For example, primary tiller 3 was a tiller that developed from node 3 of the main tiller and so emerged from the sheath of leaf 3 on the main tiller. Secondary tillers (i.e. a tiller that developed from a node of a primary tiller) and tillers of higher order of each individual primary tiller were counted. They were defined as branch tillers. Each primary tiller and its branch tillers were called a colony. The production of leaves of each primary tiller was recorded in the same manner as for the main tiller. These leaves were nevertheless not tagged and the first leaf appearing was considered as leaf number 1. Number of dead leaves of each primary tiller was recorded at only three dates (7/17, 7/31 and 8/14 for plants of treatments 1 and 2; 7/24, 8/7 and 8/18 for plants of treatments 3 and 4). For branch tillers in each colony, it was registered on 8/14 for plants of treatments 1 and 2 and on 8/18 for plants of treatments 3 and 4.

1.5. Destructive morphological measurements

Height was measured for the main tiller and each primary tiller from the base of the stem until the tip of the last leaf.

Individual mature leaf blade was measured non-destructively with a leaf area meter (MK2; Delta-T Devices Ltd, Cambridge, UK) at each sampling date for the main tiller. On July 17, July 31 and August 14 in the treatments 1 and 2 and on July 24, August 7 and August 18 in the treatments 3 and 4, it was also measured for each individual primary tiller, on August 14 in treatments 1 and 2 and on August 18 in treatments 3 and 4 for branch tillers in each individual colony.

After the leaves were numbered, tillers counted, tiller height and leaf area measured, the different parts of the plants (stems, senescent and non-senescent leaves) were put into bags and placed in an oven (70 ºC) for 24 hours. Afterwards, each sample was weighed. Stems consisted in nodes, internodes and leaves' sheath, leaves were restricted to their blade.

At maturity, the groups of seedlings which were not used for the destructive measurements during the growth period were taken to determine the yield components per primary tiller's colony and for the main tiller. Three groups in treatments 1 and 2 and one group in treatments 3 and 4 were remaining. The parameters taken into account were stem length, stem number and dry weight, leaf dry weight, panicle number and dry weight, filled and unfilled grains dry weight, and 100 filled grains and unfilled grains dry weight when it was possible (else a determined number of grains were weighed). Parameters were taken for colonies of each primary tiller (primary and branch tillers together) and for main tillers. Number of productive primary tillers and branch tillers in each colony was also counted separately. In the treatments 3 and 4, two more untagged groups were taken to determine yield components of whole plant. Main stem length, total number of tillers, number of productive tillers, stem and leaf dry weight, panicle number and dry weight, filled and unfilled grain dry weight, and dry weight of one thousand filled and unfilled grains (when it was possible) were measured.

1.6. Validity of the results

The treatments 1, 3 and 4 were also realized in the same conditions (same field, same date of sowing, IR 72) on the whole plant in order to measure yield on big areas (>37 m^2). Primary tillers were not considered individually in this experiment noted experiment 1 and treatments consisted of a large range of varieties. To test the validity of the results a comparison of yields and harvest index HI (dry weight of the grains per unit of total dry weight produced) between both experiments was made (**Fig.1.**). In experiment 1, yield was measured from the harvest area; in experiment 2 (exposed in this report), it was calculated from the yield components measured. In all treatments, yield and HI were lower in experiment 2. It might be attributed to tagging which needed a manipulation of the plants. For yield it might also be due to the difference in the calculation method. Anyway, plants in treatments 1, 3 and 4 were affected in the same way in experiment 2 and comparisons between treatments could be made.

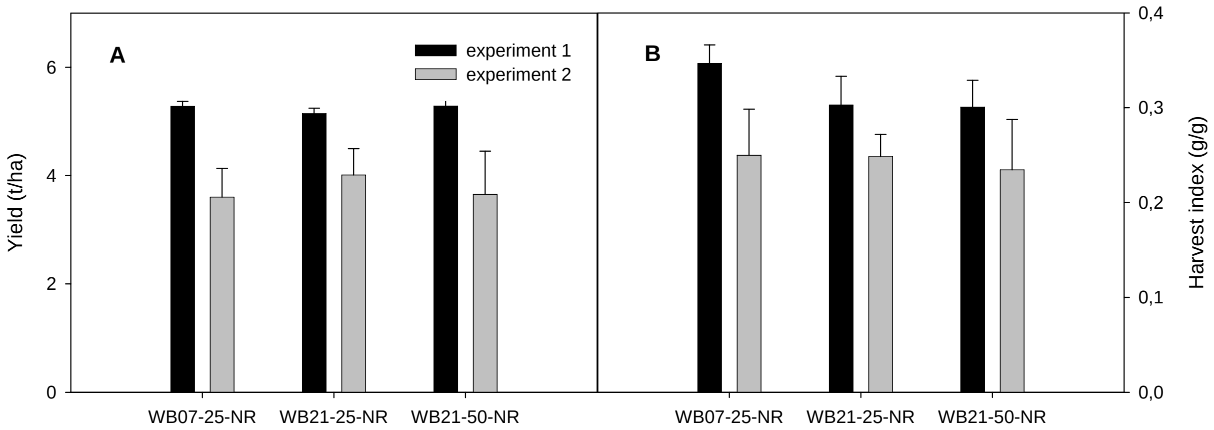


Fig.1. Comparison of the yield and the HI between two experiments in the same location differing by a tagging (exp1) or not (exp2) of each individual primary tiller, considering treatments 1, 3 and 4.

2- RESULTS

2.1. Tillering dynamic of plants transplanted at 7 DAS at a density of 25 m^{-2}

At the whole plant's scale, the most numerous tillers were unproductive at the greatest rate. Tillers appearing late were the lightest ones.

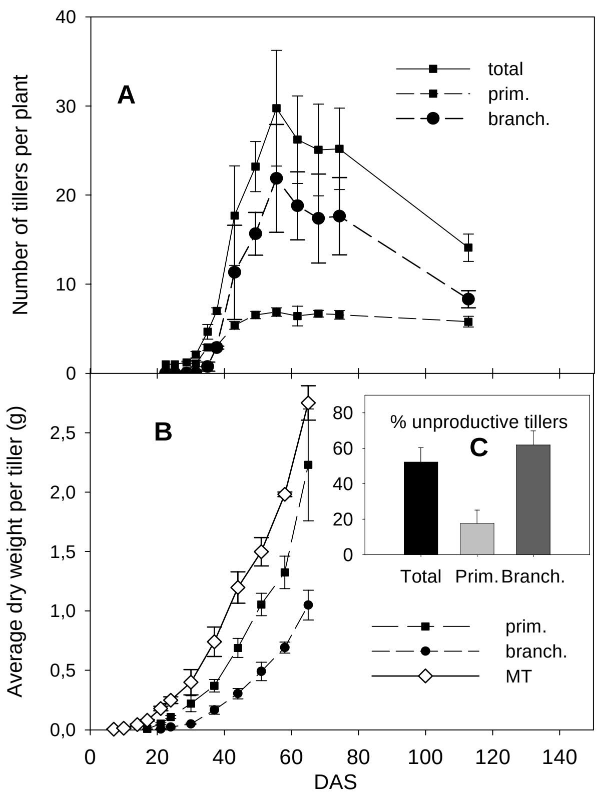


Fig. 2. Tillering dynamic of plants in WB 07-25-NR considering all (*total*), primary (*prim.*)and branch tillers *(branch.*). **A**: Number of tillers per plant, **B**: Average dry weight per tiller (main tiller MT included), **C**: Percentage of unproductive tillers.

Plant synthesized tillers first in an exponential way until about 15 DAS, then in a linear pattern until maximum tillering (about 45 DAS) (**Fig. 2A.**). Tillers began afterwards to die and just one part of the remaining tillers gave grains: from the 30 tillers synthesized, only 15 were productive. Tillers appearing were first main tillers, then primary tillers and finally branch tillers. Both were synthesized with the same dynamic as the one exposed above. Tiller appearance rate was lower for primary tillers, higher for branch tillers. As a consequence, since maximum tillering occurred at about the same time for primary and branch tillers, maximum number of tillers was lower for primary tillers (less than 7 per plant, against more than 20 per plant for branch tillers). The higher number of branch tillers synthesized were also the most unproductive : only 40 % produced grains unlike 80 % for primary tillers (**Fig. 2C.**).

Average dry weight between tillers was compared in **Fig. 2B.**. Only the values before 40 DAS were considered since, after that date, tillers stopped their development and then died in a lower proportion for primary than for branch tillers. So, before 40 DAS, main tiller was on average heavier than each primary tiller which were also heavier than branch tillers. It was the same hierarchy as the one observed for the dates of tillers emergence. After 40 DAS, the end of growth of some tillers engendered an increase in the difference of average dry weight between primary and branch tillers.

The frequency of each individual primary tiller and the number of branch tillers per colony at maximum tillering decreased as colony number increased, except for T3 and T4. The same hierarchy was also observed for the percentage of unproductive tillers and the number of productive tillers at harvest.

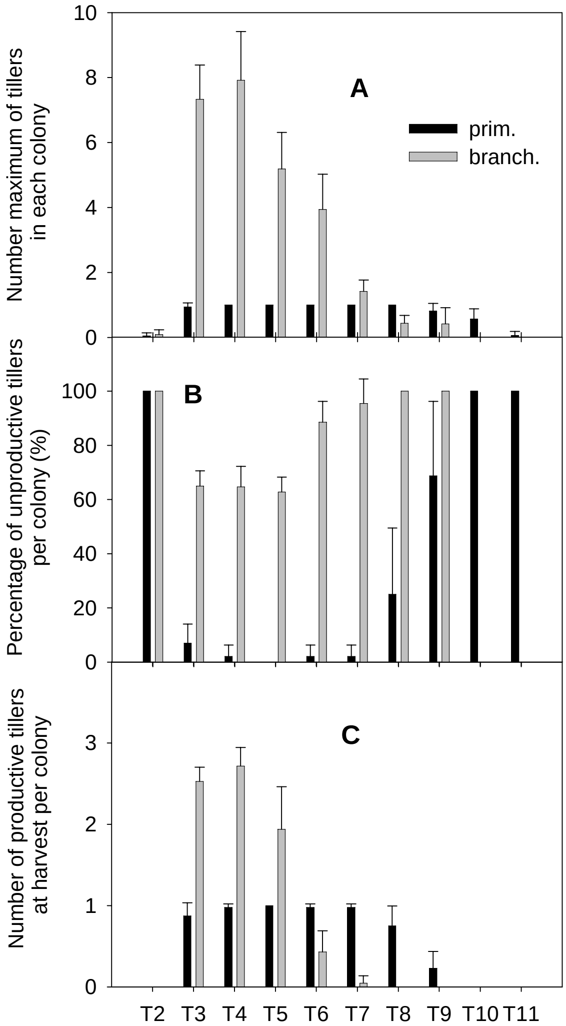


Fig 3. Productive and unproductive tillers in each individual colony *T2, T3, …*of plants in WB 07-25-NR. **A**: Number maximum of tillers, **B**: Percentage of unproductive tillers, **C**: Number of productive tillers at harvest. Primary tillers (*prim.*) and branch tillers (*branch.*) were separated.

The main tiller's leaf from which emerged the primary tiller which had the lower number was generally leaf 3 (**Fig. 3A**) : T3 (primary tiller 3) was present at about 94 %. T2 was sometimes existing (5 %). The frequency of the last primary tillers (those with a higher number) decreased as their number increased : 81 % for T9, 56 % for T10 and 6 % for T11. In the same way, maximum number of branch tillers per primary tiller decreased as colony number increased : T3 and T4 had about 8 tillers in their colony, T5 about 5, T6 about 4, T7 less than 2, T8 and T9 less than 1 and T10 and T11 had none. Branch tillers in the existing colonies were unproductive in a higher percentage than their primary tiller (**Fig. 3B.**), that confirmed what was observed above at the whole plant's scale (Fig.3.). Percentage of unproductive tillers increased also with colony number. Primary tillers T8 were unproductive at 30 %, T9 at 60 % and T10 and T11 at 100 %. About 60 % of the tillers in colonies 3, 4 and 5 were unproductive, whereas more than 85 % were unproductive in colonies 6, 7, and tillers in colonies 8 and 9 (where primary tillers were not always productive) were all unproductive. As a result, at harvest, the most productive colonies were those with a lower number (**Fig. 3C**). Primary tillers T3 to T7 were almost all productive unlike T8 and T9 which were productive at more and less than 50 % respectively. More than 2.5 tillers were also productive in T3 and T4, 2 in T5 and T6 and T7 had not always productive tillers in their colony.

The productivity of one colony was related to the number of productive tillers.

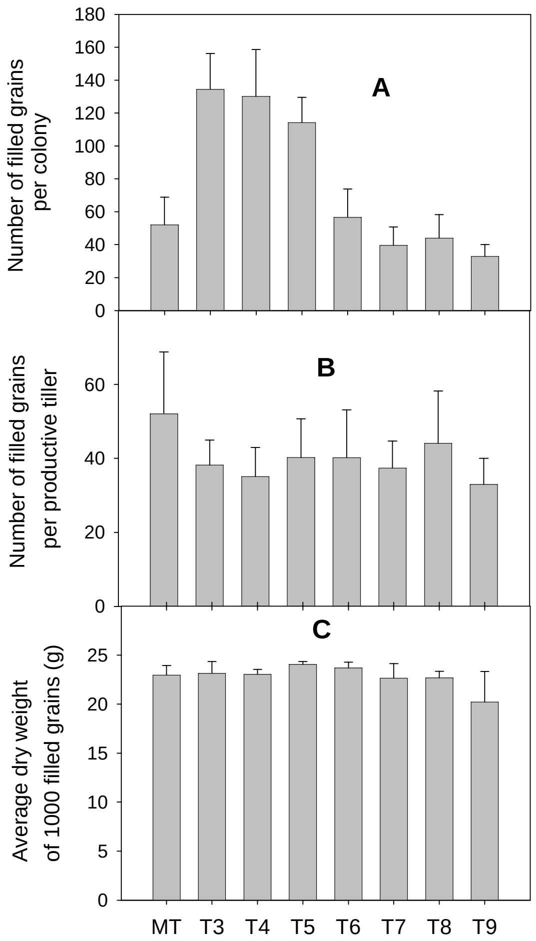


Fig. 4. Productivity of the main tiller and of each individual colony T3, T4, … of plants in WB 07-25-NR. **A**: Total number of filled grains per colony. **B**: Number of filled grains per productive tiller. **C**: Average dry weight of 1000 filled grains.

The most productive colonies were those with a lower number (**Fig. 4A.**). Total number of filled grains was higher for T3, T4 and T5 (135, 130 and 114 respectively) and lower for T6, T7, T8 and T9 (less than 60). Main tiller produced about 50 filled grains. These differences of filled grains' number between colonies were the result of productive tillers' number per colony. On the one hand, number of filled grains per productive tiller did effectively not vary so much between colony (**Fig. 4B.**). It was slightly higher for the main tiller (50) and lower for the last primary tiller T9 (33). T4, which had the higher number of tillers in its colony (Fig. 3B.), may also have less filled grains per productive tiller. On the other hand, grain's average dry weight was similar between colonies (**Fig. 4C.**), except for grains of the last tiller which were slightly lighter.

Primary tillers emerged in a regular order. Number of leaves was different between main tiller, T3, T4 and T5 but height and dry weight were similar.

Fig. 5A. shows an order in each primary tiller's emergence : primary tiller n appeared before primary tiller n+1. Number of leaves on each primary tiller increased at the same rate. Consequently, no primary tiller had a higher number of leaves than the one that appeared earlier all over the growing period. Nevertheless, T3 had a lower rate of leaf appearance after maximum tillering and number of leaves became equal to T4. After 50 DAS, leaf appearance rate of each primary tiller decreased. Tiller growth was expressed through an increase in number of leaves, its dry weight became also greater all over the growing period (**Fig. 5B.**).Dry weights of main tiller, T3, T4 and T5 were similar. For tillers of higher number, dry weight decreased as tiller number increased. The difference between T7 and T8 became greater after 50 DAS, percentage of unproductive tillers was effectively significant for T8. Height was the other index of growth of each primary tiller (**Fig. 5C.**). Heights of main tiller, primary tillers T3, T4, T5 and T6 became also equal. For primary tillers of higher order, height decreased as tiller number increased. As dry weight of each primary tiller, average dry weight of one tiller in each colony was equal for T3, T4 and T5 and lower for T6 (**Fig. 5D.**).

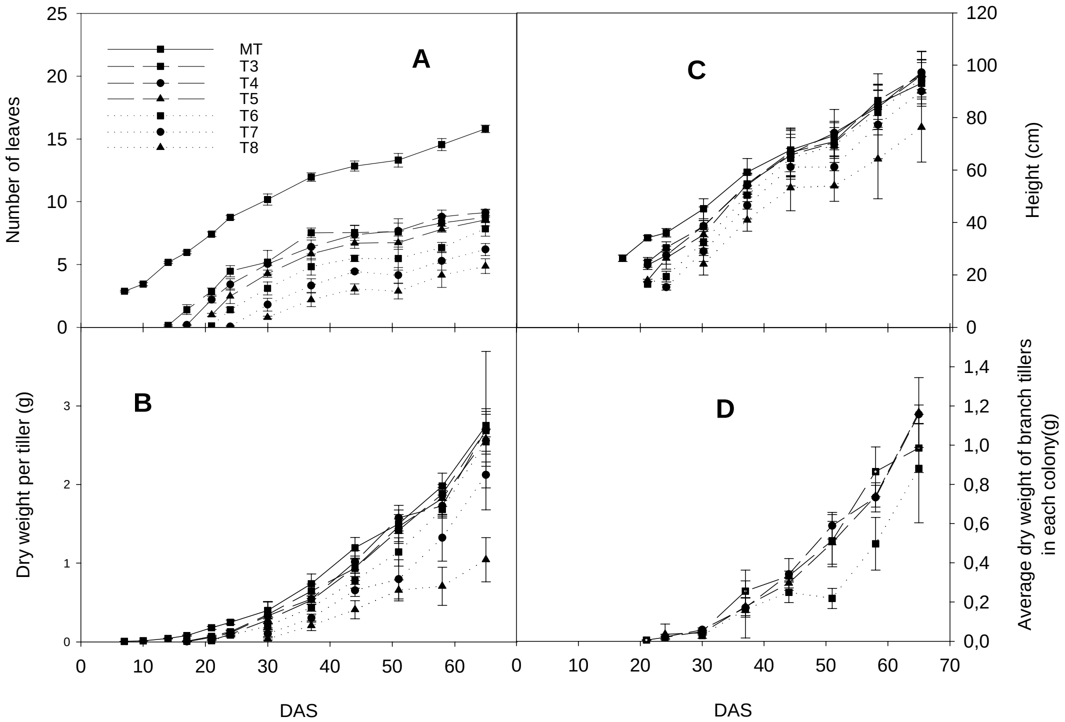


Fig. 5. Growth dynamic of the main tiller (*MT*) and of each individual colony T3, T4, … of the plants in WB 07-25-NR. Were considered : number of leaves (**A**), average dry weight (**B**) and height (**C**) of each primary tiller and of the main tiller, average dry weight of the branch tillers of each colony (**D**).

2.2. Effect of the removal of the first primary tillers appearing

Plants which first primary tillers had been removed synthesized a lower number of tillers- which were also lighter and unproductive at a greater rate- and of productive tillers. Timing of the phenological stages was not affected.

Removal of primary tillers 2, 3 and 4 resulted in a lower number of tillers per plant until about 50 DAS (**Fig. 6A**). At this time number of tillers was similar in both treatments (about 25 tillers per plant). Maximum tillering occurred effectively a little bit later in treatment 2 and tillers in treatment 1 had already begun to die. On the contrary, dates of panicle initiation, flowering and maturity were not affected by tillers' removal. Quite same number of tillers was unproductive in both treatments. As maximum tillering was lower in WB 07-25-TR, less tillers were productive at harvest and percentage of unproductive tillers was higher in this treatment (about 68 % in treatment 2, 52 % in treatment 1) (**Fig. 6D**). Primary and branch tillers were both affected by this higher rate of unproductive tillers : they had respectively 18 % and 62 % of unproductive tillers in treatment 1 and 36 % and 75 % in treatment 2. Increase in number of primary and branch tillers

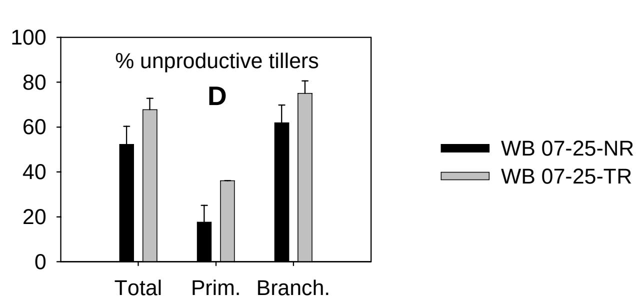


Fig. 6D. The differences in tillering dynamics of WB 07-25-NR and WB 07-25-TR : percentage of unproductive total, primary (*prim.*) and branch tillers (*branch.*)

showed the same patterns as at the whole plant's scale (**Fig. 6B**). All, primary and branch tillers had an average dry weight lower in treatment 2. Plants synthesized lighter tillers in this treatment (**Fig. 6C.**). At harvest, average dry weight per tiller became higher in WB 07-25-TR : the lighter tillers synthesized might have been not productive.

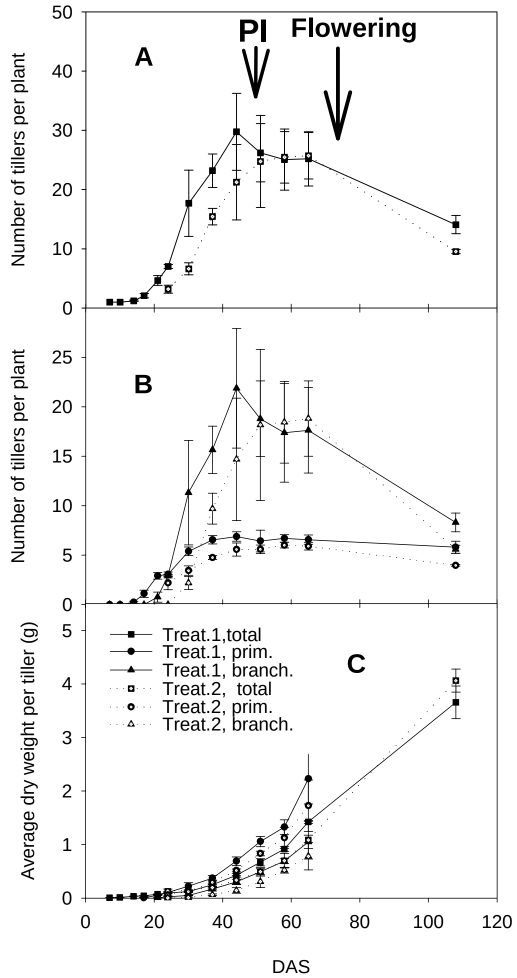


Fig. 6. Differences in tillering dynamics of treatments 1 and 2 (*Treat.1*, *Treat.*2). All (*total*), primary (*prim.*) and branch (*branch.*) tillers were separated. **A**: Total number of tillers per plant, **B**: Number of primary and branch tillers per plant, **C**: Average dry weight per tiller. *PI= Panicle initiation.*

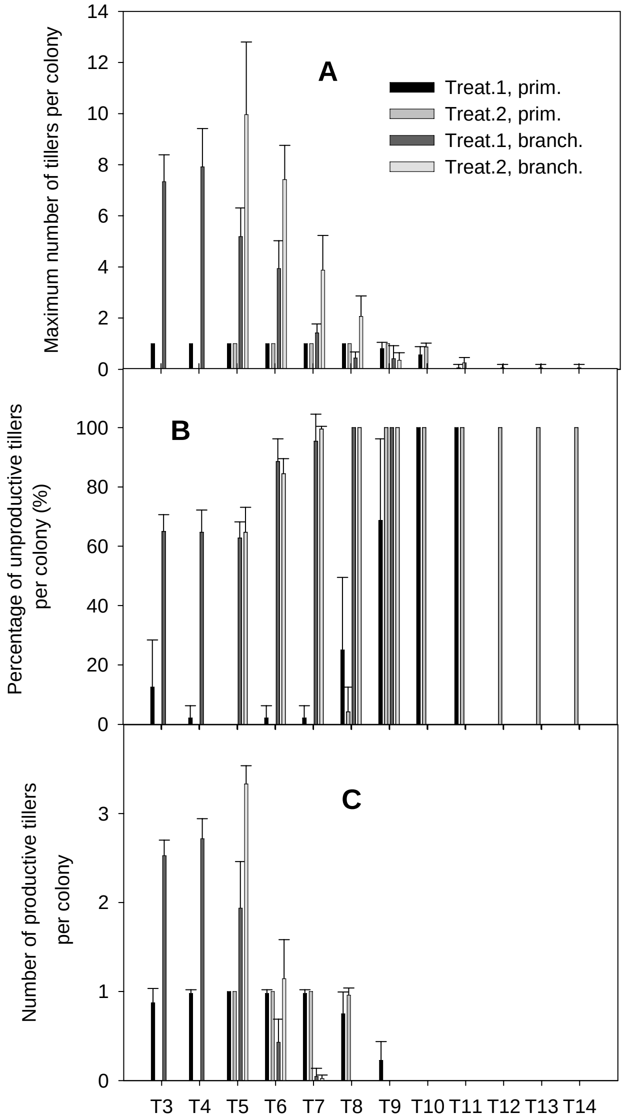


Fig. 7. Differences of productive and unproductive tillers in each colony T3, T4, … between treatments 1 and 2 (*Treat.1*, *Treat.*2).. **A**: Number maximum of tillers, **B**: Percentage of unproductive tillers, **C**: Number of productive tillers. Primary (*prim.*) and branch (*branch*) tillers were separated.

Plants which tillers had been removed synthesized more branch tillers in the colonies 5 and 6, percentage of unproductive tillers did not vary and number of productive tillers was double in those colonies.

Primary tillers of higher number were present at maximum tillering (**Fig. 7A**) : they existed at almost 100 % until T10 in treatment 2 unlike T9 in treatment 1. Number of tillers in the colony was also more than the double in treatment 2 compared to treatment 1 until T8 included. In treatment 2, total number of primary and branch tillers was nevertheless lower because of the removal of primary tillers 2, 3 and 4 (Fig. 6B). Percentage of unproductive primary tillers was lower for the first primary tillers formed (T5 to T8) in treatment 2 (**Fig. 7B**). None of T5, T6 and T7 were unproductive and only 4 % of T8 were unproductive. A big difference existed with the following tillers (from T9 to T14) which were all unproductive. This unproductive late formed primary tillers were responsible for the total high percentage of unproductive primary tillers in treatment 2 (36 %, Fig. 6D). In treatment 1, the increase in the percentage of unproductive primary tillers was more progressive : 2 % for T7, 25 % for T8 and 69 % for T9. Percentage of unproductive branch tillers in each colony was similar between treatments. On average, it was higher (Fig. 6D) : only T5 effectively had unproductive tillers at a quite lower rate (60 %) in treatment 2, whereas T3, T4 and T5 had this lower rate in treatment 1. Unproductive tillers were tillers of colonies of higher number. As a result (**Fig. 7C**), at harvest, primary tillers existed in a lower range in treatment 2 compared to treatment 1 (from T5 to T8 and from T3 to T9, respectively) but were always present (in treatment 1, T8 existed at 75 % and T9 at only 23 %) and the existing colonies 5 and 6 had two times more branch tillers.

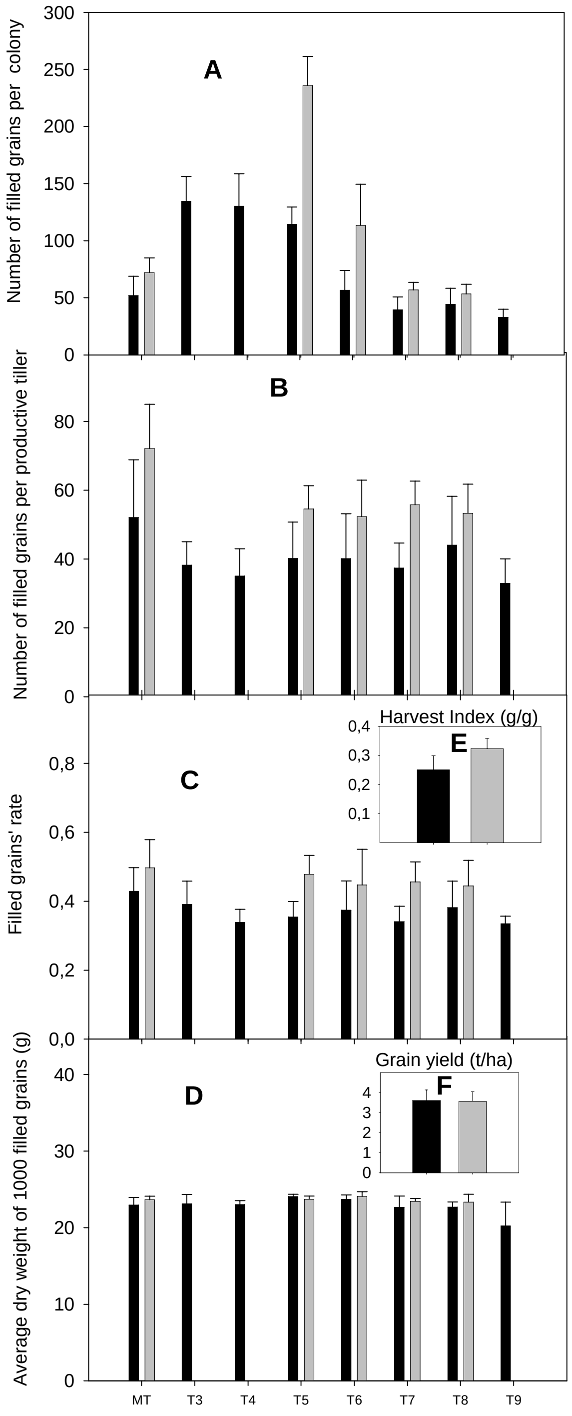


Fig. 8. Differences in productivity of the main tiller and of each individual colony T3, T4, … between treatments 1 and 2 (*Treat.1*, *Treat.2*). **A**: Number of filled grains per colony, **B**: Number of filled grains per productive tiller, **C**: Percentage of filled grains, **D**: grains' average dry weight, **E**: Harvest Index**, F**: Yield computed from the yield components.

In treatment 2, plants had a higher filled grains' rate and harvest index, colonies 5 and 6- which had the more numerous productive branch tillers- were the most productive : yield was similar between treatments.

Main tiller and each individual colony 5, 6, 7 and 8 produced more filled grains in treatment 2 (72, 236, 113, 57 and 53 grains respectively) than in treatment 1 (52, 114, 57, 40 and 44 respectively) (**Fig. 8A**). Main tiller produced effectively on average more grains and average number of filled grains per productive tiller in each of those individual colonies was greater in this treatment (**Fig. 8B**). This was the result of a higher percentage of filled grains in each colony which had 44 to 50 % of filled grains in treatment 2 and 34 to

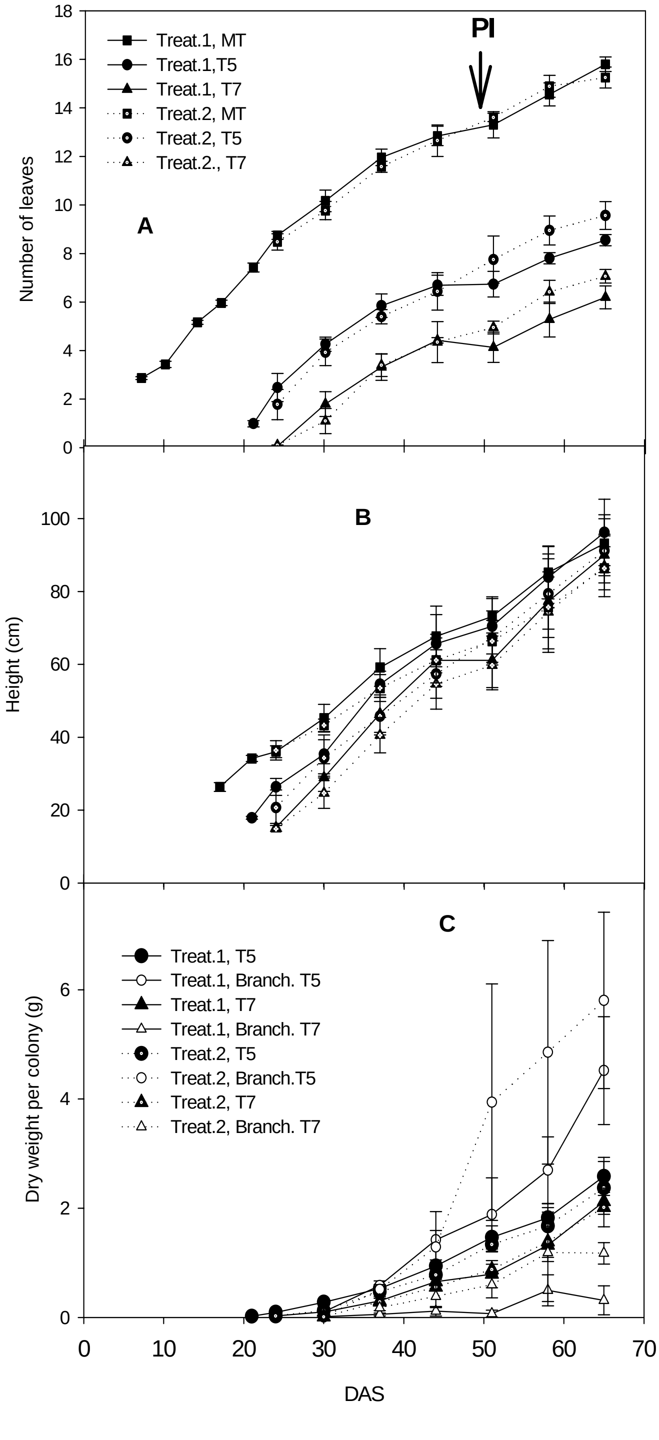


Fig. 9. Differences in growth dynamic of each individual colony T5, T7 and of the main tiller (*MT*) between treatments 1 and 2 (*Treat.1, Treat.2*). **A**: Number of leaves, **B**: Height**, C:** average dry weight. A and B only considered the main tiller and the primary tillers (*prim.*), C included branch tillers (*branch.*) and excluded main tiller. *PI= Panicle initiation.*

43 % of filled grains in treatment 1 (**Fig. 8C**). Differences in number of filled grains per colony 5 and 6 were greater than in the other colonies : it was related to the number of productive tillers per individual colony double in treatment 1 compared to treatment 2. These higher values per individual colony compensated the total lower number of productive tillers per plant at harvest and total number of filled grains per plant was similar between treatments (between 500 and 600). Grains' average dry weight remained equal between treatments and colonies (**Fig. 8D**) and harvest index was higher in treatment 2 (0.32g/g; 0.25 g/g for treatment 1) (**Fig. 8E**). As a result grain yield calculated from these yield components was about 3.5 in both treatments (**Fig. 8F**).

Leaf appearance rate of each individual primary tiller and dry weight of the branch tillers in each colony became higher after 50 DAS whereas height was lower in treatment 2.

Number of leaves was similar until panicle initiation between both treatments (**Fig. 9A**). At this time, increase in number of leaves of T5 and T7 slowed down in treatment 1 unlike in treatment 2 where number of leaves became then higher. Main tiller was not affected by this slowdown. Height of the main tiller, T5 and T7 was nevertheless slightly higher in treatment 1 all over the growing period (**Fig. 9B**) and dry weight of primary tillers 5 and 7 were not different between treatments (**Fig. 9C**). Tillers removal had an effect on the dry weights of the branch tillers of each colony : they became superior in treatment 2 after 50 DAS as it had been observed at harvest for the number of branch tillers in each of those colonies (Fig. 8A).

2.3. The effect of transplanting plants of 21 DAS instead of 7 DAS

The timing of the phenological stages was delayed in treatment 3. Less and lighter tillers were synthesized, a lower percentage was unproductive and number of productive tillers and their average weight were similar in both treatments.

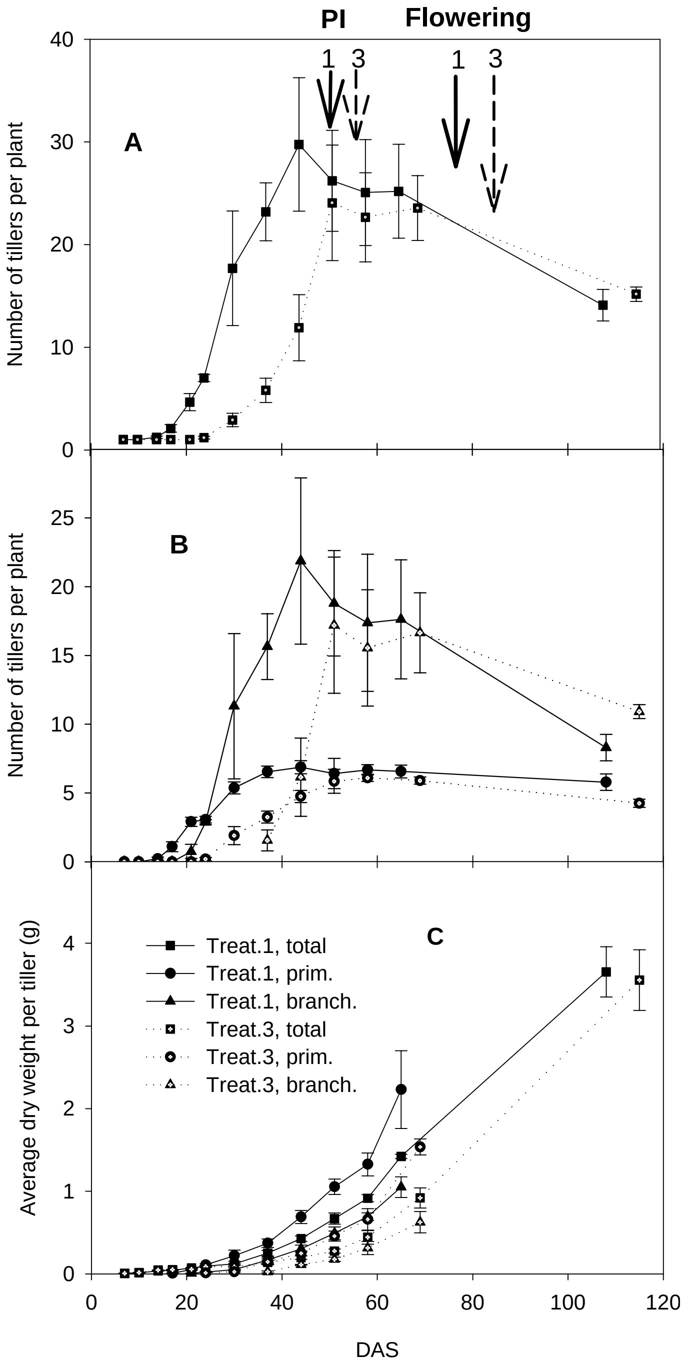


Fig. 10. Differences in tillering dynamics of treatments 1 and 3 (*Treat.1*, *Treat.*3) considering all (*total*), primary (*prim.*) and branch (*branch.*) tillers. **A**: Total number of tillers per plant, **B**: Number of primary and branch tillers per plant, **C**: Average dry weight per tiller. *1=treatment1, 3=treatment3; PI=Panicle initiation.*

Tillers did not appear during the stage in the nursery (**Fig. 10A.**). So, in WB 21-25-NR, number of tillers began to increase later and remained lower until maximum tillering : plant's growth was delayed. As maximum tillering was delayed of about 7-8 days in WB 21-25-NR, plants were able to achieve a higher number of tillers than the one they had at the time of maximum tillering of WB 07-25-NR. Nevertheless, delay was not sufficient to achieve the same maximum number of tillers as in treatment 1. Finally, number of tillers of the plants in treatment 3 at maximum was similar to the one in treatment 1 since tillers in this treatment have already begun to die. Panicle initiation, flowering and maturity were also delayed (5, 8, 7 days respectively) when plants had been transplanted late. At harvest, total number of tillers were almost the same in both treatments (about 15 tillers/plant). Primary and branch tillers had also the same dynamic as the one described before (**Fig. 10B.**). Differences existed between the rate of tiller appearance : it was lower for primary tillers and greater for branch tillers in WB 21-25-NR than in WB 07-25-NR. Number of primary tillers was also lower at harvest in treatment 3 compared to treatment 1, it was the opposite for branch tillers.

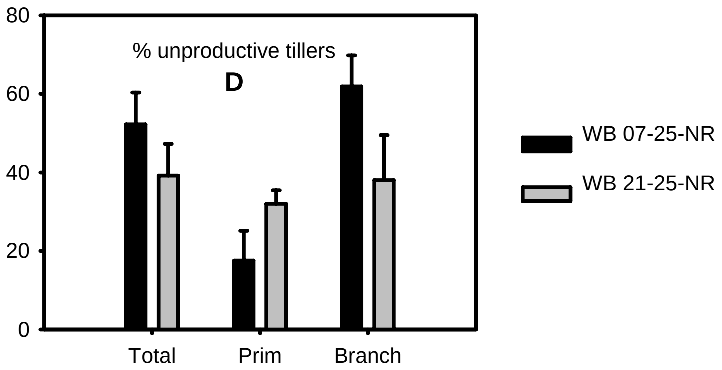


Fig. 10D. Differences in tillering dynamics of WB 07-25-NR and WB 21-25-NR : percentage of all, primary (*prim.*) and branch unproductive tillers (*branch.*)

This was the result of the differences in percentages of unproductive tillers (18 % and 62 % in treatment 1; 32 % and 38 % in treatment 3, for primary and branch tillers respectively) (**Fig 10D.**). At the whole plant's scale, percentage of unproductive tillers was higher in WB 07-25-NR. Average dry weight of primary and branch tillers was lower in WB 21-25-NR (**Fig. 10C.**). Until maturity, plants produced lightest tillers when they had been transplanted late. At maturity, delay in maturity dates and senescence percentage engendered the same average dry weight.

Less tillers were present in each colony of treatment 3 but less branch tillers died in the colonies 3 and 4 which had more productive tillers at harvest.

Plants synthesized less tillers per individual colony in treatment 3 (**Fig. 11A.**). First, a lower range of primary tillers were present at maximum tillering : primary tillers T8 were present at 95 % in WB 21-25-NR, they were always present in WB 07-25-NR. Frequency of T9 were also lower and T10 did not exist in treatment 3. Then, number of branch tillers in each colony was lower in WB 21-25-NR. Percentage of unproductive primary tillers became significant from T7 (75 %) in WB 21-25-NR whereas its increase with tiller number was more progressive and occurred later in the other treatment (25 % for T8, 70 % for T9) (**Fig. 11B.**). Percentage of unproductive branch tillers was lower for colonies 3 and 4 in treatment 3. As a result, at harvest, plants in WB 21-25-NR had a lower range of primary tillers (T3, T4, T5 and T6 were always existing; T7 was present at only 25 %) (**Fig. 11C.**). The drop in the frequency of each primary tiller was also more obvious than in the other treatment (75 % of T8 were present and 23 % of T9). Branch productive tillers were more numerous in WB 21-25-NR in colonies 3 and 4 and less numerous in colony 5. The high number of tillers in colonies 3 and 4 explained the total high number of productive tillers observed previously.

Both treatments had the same productivity because of the higher number of filled grains of colonies 3 and 4 that compensated the absence of colony 8 and 9 in treatment 3.

Number of filled grains was higher in the colonies 3, 4 and 7 in WB 21-25-NR and similar between both treatments for the other tillers present and for the main tiller (**Fig 12A.**). Number of filled grains per productive tiller was slightly higher in treatment 3 but it was not significant except for the colony 7 (**Fig. 12B.**) Percentages of filled grains had the same pattern (**Fig. 12C.**). Number of filled grains per productive tiller was so explained by the percentage of filled grains, the higher number of grains per colony 3, 4 and 7 resulted from a higher number of tillers per colony 3 and 4 and a higher percentage of filled grains for colony 7. The higher numbers of filled grains for colonies 3, 4 and 7 compensated the absence of tillers 8 and 9 in WB 21-25-NR. Average dry weight of grains was also similar between treatments (**Fig. 12D.**). As a result, plants in both treatments had the same productivity (**Fig. 12E.**).

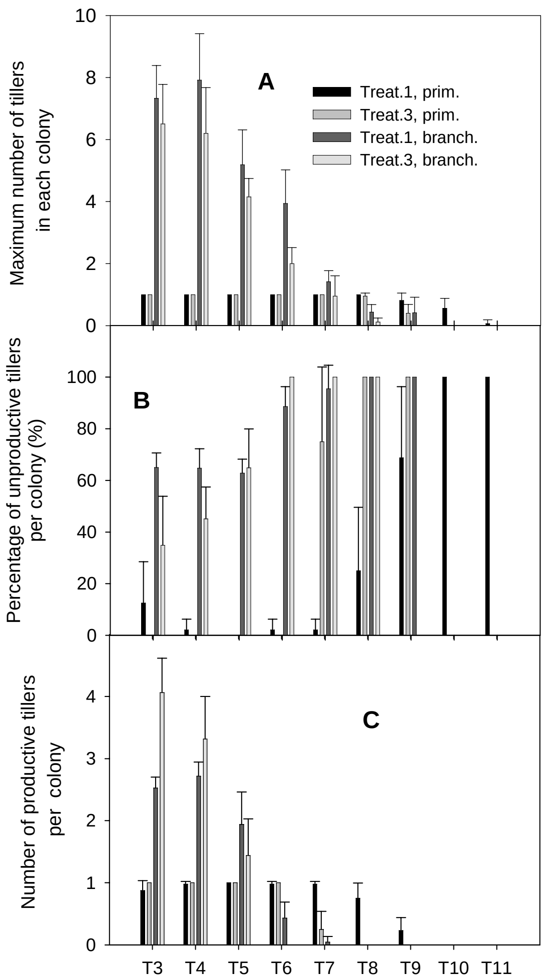


Fig. 11. Differences of productive and unproductive tillers in each colony T3, T4, … between treatments 1 and 3 (*Treat.1*, *Treat.3*). **A**: Number maximum of tillers, **B**: Percentage of unproductive tillers, **C**: Number of productive tillers. Primary (*prim.*) and branch (*branch*) tillers were considered separately.

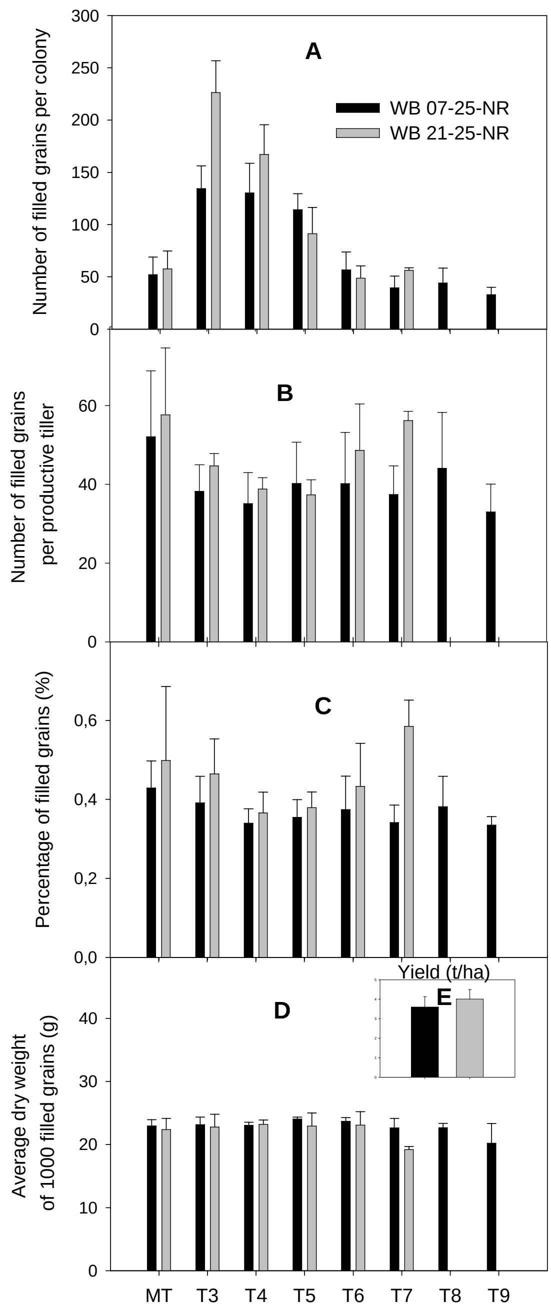


Fig. 12. Differences in productivity of the main tiller and of each individual colony T3, T4, … between treatments 1 and 3 (*Treat.1*, *Treat.3*). **A**: Number of filled grains per colony, **B**: Number of filled grains per productive tiller, **C**: Percentage of filled grains, **D**: grains' average dry weight, **E**: Yield computed from the yield components.

Delaying plant's age at transplanted resulted in a delay in appearance of the main, each primary and its corresponding branch tillers.

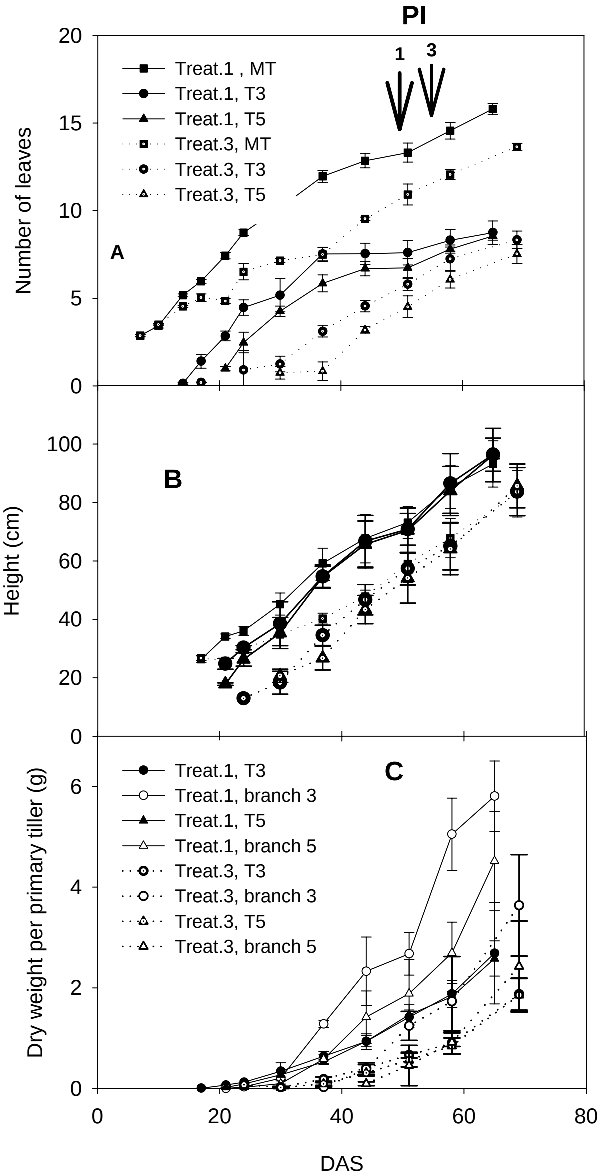
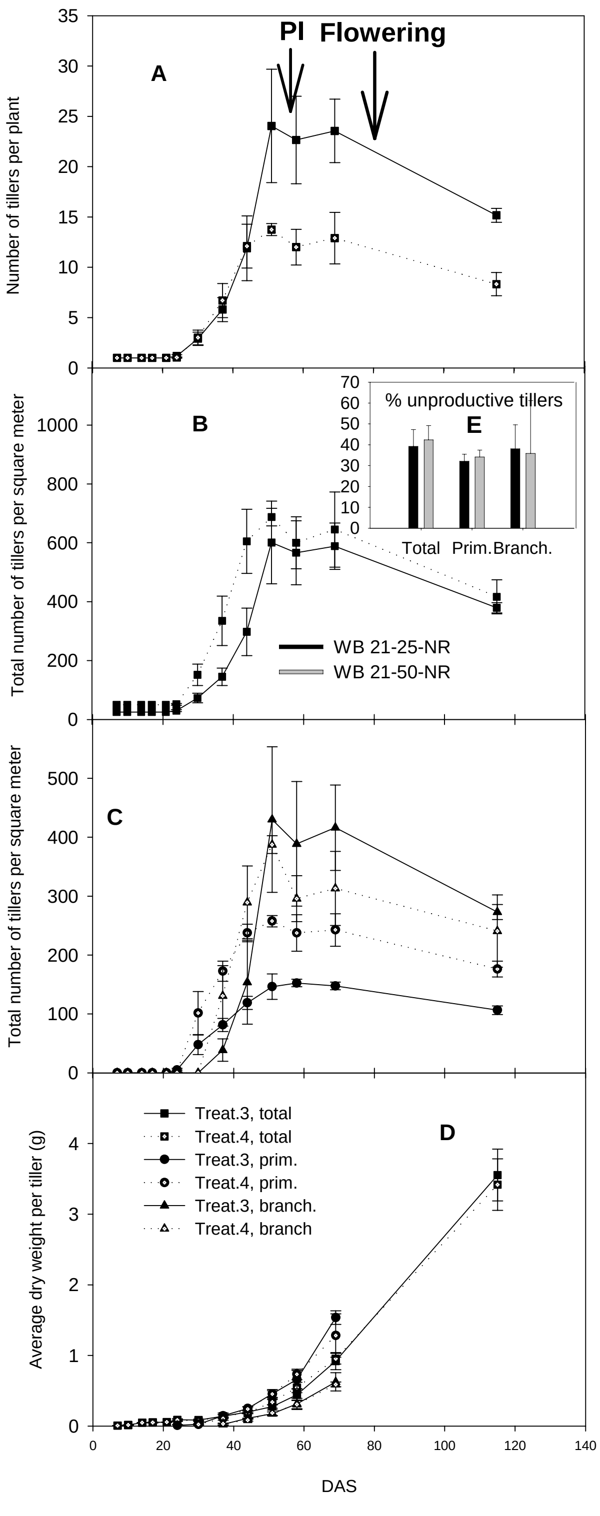


Fig. 13. Differences in growth dynamic of each individual colony T3, T5 and of the main tiller (*MT*) between treatments 1 and 3. **A**: Number of leaves, **B**: Height**, C:** average dry weight. A and B only considered the main tiller and the primary tillers (*prim.*), C included branch tillers (*branch.*) and excluded the main tiller. *PI 1= panicle initiation for treatment 1, PI 3= panicle initiation for treatment 3.*

Unlike the global constant rate of main tiller's leaves' appearance observed in WB 07-25-NR (**Fig. 13A.**), the one in WB 21-25-NR began to slow down while the plants were still in nursery to finally become equal to 0 before 21 DAS. Then transplanting made this rate become higher than in WB 07-25-NR. After 37 DAS, leaf appearance rate on the main tiller was quite similar between both treatments. This perturbation was not visible for primary tillers 3 and 5, they appeared effectively later in treatment 3 and were not yet present during the nursery period. Nevertheless, after 50 DAS, their leaf appearance rate became higher in treatment 3 than in treatment 1 because of the slowdown in leaf appearance observed for primary tillers in WB 07-25-NR (Fig. 5A). Height of main and primary tillers 3 and 5 were similar after 40 DAS and always lower in treatment 3 (**Fig. 13B.**). Delaying plant's age at transplanting also resulted in lighter primary tillers 3 and 5 and lighter branch tillers in their colony (**Fig. 13C.**). These lower values were a consequence of a delay in the emergence of each tiller and its corresponding branch tillers.

2.4. The effect of tranplanting plants at 50 plants m^{-2} instead of 25 plants m^{-2}

Tillering dynamic until maximum tillering and timing of the phenological stages did not change with an increase in transplanting density. The occurrence of maximum tillering slightly earlier resulted in a lower number of tillers per plant but a similar number of tillers m^{-2}.



Until maximum tillering, tiller appearance rate did not vary between treatments but tillers stopped being synthesized 3 or 4 days earlier in the highest density treatment (**Fig. 14A..**). Hence, maximum number of tillers per plant was almost double in WB 21-25-NR (about 24) compared to WB 21-50-NR (about 14) and number of those tillers which were productive at harvest was also about two times greater (15 plants in WB 21-25-NR and 8 plants in WB 21-50-NR). The timing of the phenological stages was not affected : panicle initiation and flowering occurred at 55 DAS and 83 DAS respectively, crop duration was not modified and maturity occurred at 115 DAS in both cases. Per square meter basis, before maximum tillering of plants in treatment 3, total number of tillers was about two times higher in treatment 4, it became almost similar or slightly higher afterwards (**Fig. 14B.**), percentage of unproductive tillers remaining also equal (**Fig. 14E.**). At this level, no big differences occurred between primary and branch tillers : percentage of unproductive tillers was around 35 % for both tiller types and both densities. A similar tillering dynamic as the one observed at the whole plant's scale existed for primary and branch tillers considered separately (**Fig. 14C**) but percentage of tillers of each type was different : number of primary tillers m-2 was lower in WB 21-50-NR whereas both treatments had the same number of branch tiller m-2. All over the growing period, average dry weight per tiller, per primary tiller and per branch tiller remained similar between treatments (**Fig. 14D.**).

Fig. 14. Differences in tillering dynamics of treatments 3 and 4 (*Treat.3*, *Treat.4*) considering all (*total*), primary (*prim.*) and branch (*branch.*) tillers. **A**: Total number of tillers per plant, **B**: Total number of tillers m^{-2}, **C**: Number of primary and branch tillers m^{-2}, **D**: Average dry weight per tiller, **E**: Percentage of unproductive tillers. *PI=Panicle initiation.*

Increasing density at transplanting resulted in a lower range of primary tillers and a lower number of branch tillers in each colony at maximum tillering and at harvest.

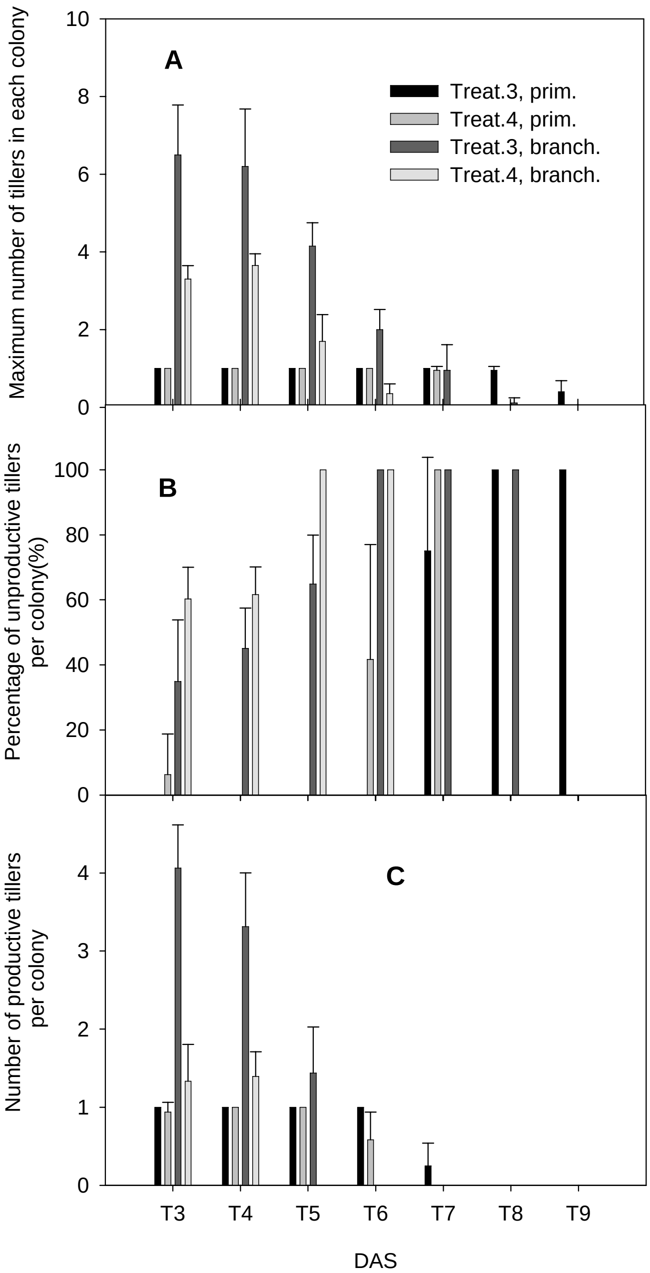


Fig. 15. Differences of productive and unproductive tillers in each colony T3, T4, … between treatments 3 and 4 (*Treat.3*, *Treat.4*). **A**: Number maximum of tillers, **B**: Percentage of unproductive tillers, **C**: Number of productive tillers. Primary (*prim.*) and branch (*branch*) tillers were considered separately.

Tillers were synthesized in a lower range in WB 21-50-NR (**Fig. 15A.**) : primary tillers were present at a high rate from T3 until T7 and branch tillers appeared until T6, whereas T8 was the last primary tiller appearing and T7 the last one having branch tillers in WB 21-25-NR Less branch tillers also appeared in each colony in treatment 4 : 50 % for colony 3, 42 % for colony 4, 60 % for colony 5 and 82% for colony 6. Each colony showed a higher percentage of unproductive tillers in WB 21-50-NR (**Fig. 15B.**).Primary tillers were unproductive from T6 at 40 % in treatment 4 and from T7 at 70 % in treatment 3. Primary tillers T7 in WB 21-50-NR and T8 and T9 in WB 21-25-NR were all unproductive. Percentage of unproductive branch tillers in the colony 3, 4 and 5 (60 %, 60 % and 100% respectively in treatment 4; 30 %, 40 % and 60 % respectively in treatment 3) was also higher in WB 21-50-NR than in WB 21-25-NR. Branch tillers in T6, T7 and T8 (when present) were unproductive at 100 %. As a result, at harvest, tillers in WB 21-50-NR were present in a lower range (**Fig. 15C.**) : primary tillers T3 to T6 (present at 58 %) and branch tillers in the colonies of T3 and T4 were productive in this treatment compared to primary tillers T3 to T7 (present at 25 %) and branch tillers in the colonies of T3 to T5 in the other treatment. Productive branch tillers in each colony T3 and T4 were also more numerous in WB 21-25-NR than in WB 21-50-NR (4 and 3.5 respectively in WB 21-25-NR, 1.3 for both in WB 21-50-NR). Productive branch tillers in each colony T3 and T4 were also more numerous in WB 21-25-NR than in WB 21-50-NR (4 and 3.5 respectively in WB 21-25-NR, 1.3 for both in WB 21-50-NR). 1.5 productive tillers was present in the colony 5 in WB 21-25-NR. Differences in number of productive tillers between both treatment decreased as colony number increased (2.7, 2.2 and 1.5 for colonies 3, 4 and 5 respectively). It resulted in a quite similar total number of productive branch tillers per square meter at harvest (Fig.

14C.) and a number of productive primary tillers per square meter two times lower in WB 21-50-NR.

Productivity between treatments was similar since it depended mainly on the number of productive tillers which was similar per square meter basis.

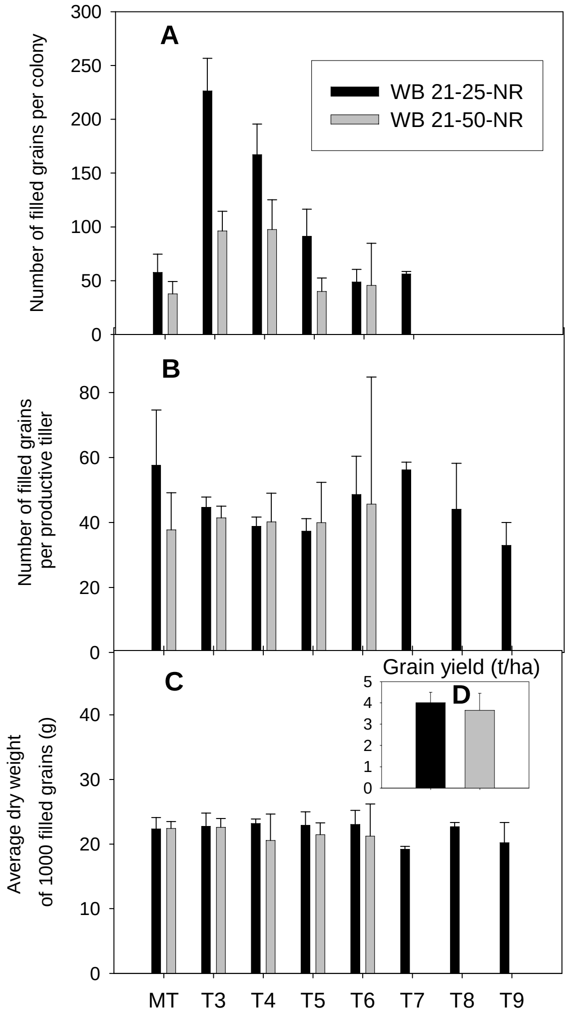
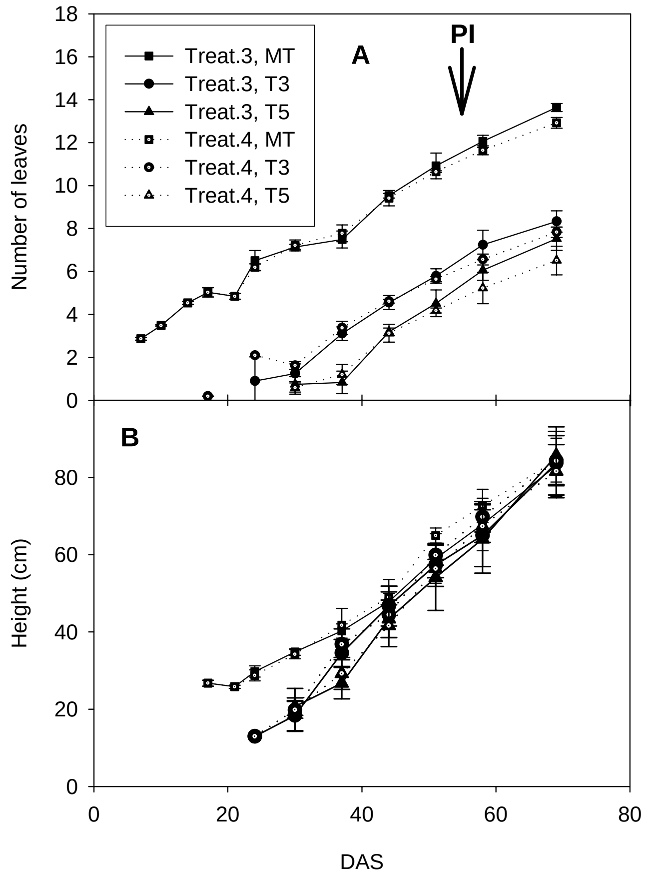


Fig. 16. Differences in productivity of the main tiller (*MT*) and of each individual colony T3, T4, … between treatments 3 and 4. **A**: Number of filled grains per colony, **B**: Number of filled grains per productive tiller, **C**: Grains' average dry weight, **D**: Yield computed from the yield components.

Tillers in the colonies 3, 4 and 5 produced more filled grains in treatment 3 (226, 167 and 91 respectively compared to 96, 97 and 39 respectively in treatment 4) (**Fig. 16A.**). Differences in number of filled grains decreased as colony number increased as it had been observed for the number of productive tillers per colony. T6 had almost the same productivity in both treatments whereas it was higher for the main tiller in WB 21-25-NR (58 filled grains against 38 in WB 21-50-NR). For the existing tillers, average number of filled grains per productive tiller did not vary significantly between treatments and colony number (**Fig. 16B.**), except for the main tiller as it had been observed above. Consequently number of filled grains per colony depended on number of productive tillers. As average dry weight of a filled grain did not vary between colony and treatments (**Fig. 16C.**), productivity depended on number of productive tillers per colony and T3, T4 and T5 were the most productive ones. Productivity was nevertheless similar between treatments (**Fig. 16D.**) : two times more productive tillers were present at harvest in WB 21-25-NR.

Growth dynamic was similar between treatments for main and primary tillers 3 and 5, except a drop in leaf appearance rate and an increase in height after 50 DAS for plants in treatment 4.



Main tiller, primary tillers 3 and 5 had the same dynamic of leaf appearance before 50 DAS (**Fig. 17A.**). After this, leaf appearance rate decreased in WB 21-50-NR and height of each primary tiller became greater (**Fig. 17B.**).

Fig. 17. Differences in growth dynamic of each individual colony T3, T5 and of the main tiller (*MT*) between treatments 3 and 4 (*Treat.3*, *Treat.4*). **A**: Number of leaves, **B**: Height. A and B only considered the main tiller and the primary tillers (*prim.*). *PI = panicle initiation.*

2.5. Modelling approach of tillering in rice

A linear relationship stable across treatments was found between the emergence of one primary tiller and its subtending leaf : 3 leaves were separating the emergence of one tiller from its subtending leaf.

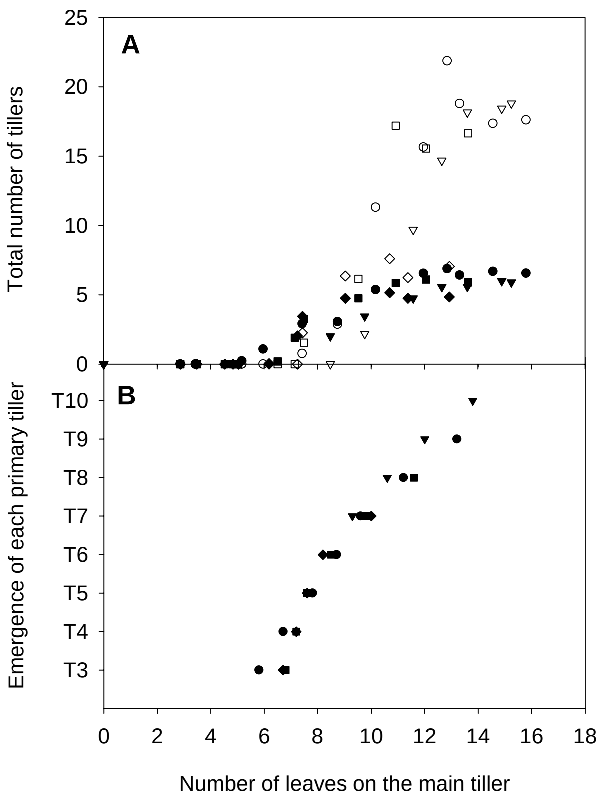


Fig. 18. Relationship between the emergence of the tillers and the number of leaves on the main tiller. The four treatments were considered : treatment 1(circles), 2 (downward pointing triangles), 3 (squares) and 4 (diamond). **A**: total number of primary (closed symbols) and branch tillers (open symbols), **B**: Emergence of each individual primary tiller T3, T4... Values were the mean of the four repetitions in each treatment.

A stable relationship across the four treatments existed between total number of primary tillers and number of leaves of the main tiller (**Fig. 18A**). Number of branch tillers also increased as number of leaves of the main increased in the same way for the four treatments. The rate of appearance (number of leaves basis) was higher and points were more dispersed for branch than for primary tillers. If each individual primary tiller was considered, their emergence increased linearly with the number of leaves on the main tiller and the rate was similar between treatments (**Fig. 18B.**) : primary tiller n emerged as leaf number n+3 was fully expanded.

Plants stopped synthesizing tillers in the four treatments at a LAI between 2 and 2.5.

Maximum tillering occurred at about the same LAI between 2 and 2.5 in treatments 1, 3 and 4. The results are presented in **Table 1**

	method 1		method 2	
Treatment	***DASmax***	***LAI***	***DASmax***	***LAI***
WB 07-25-NR	41.5	2.25	42	2.3
WB 21-25-NR	51	2.15	51	2.15
WB 21-50-NR	46	2.07	51	2.55

Table 1. Leaf area index (LAI) and dates at which maximum tillering occurred in treatments 1, 3 and 4. Two methods were used to determine maximum tillering. ***Method 1*** used the approximation by a linear function on time of the number of tillers. The date at which maximum number of tillers was achieved was defined as the date at which the regression reached the maximal number of tillers***.*** ***Method 2*** used the date at which RTR (relative tillering rate) was equal to 0. In both cases, the obtained dates gave the LAI (measures taken from the other experiment which occurred in the same conditions). *DASmax=DAS at which maximum tillering was reached.*

RGR and RTR differed in treatment 3 from the three other treatments. Plants in treatments 2 and 3 did not check the linear relationship between RTR and RGR, they showed a higher RTR.

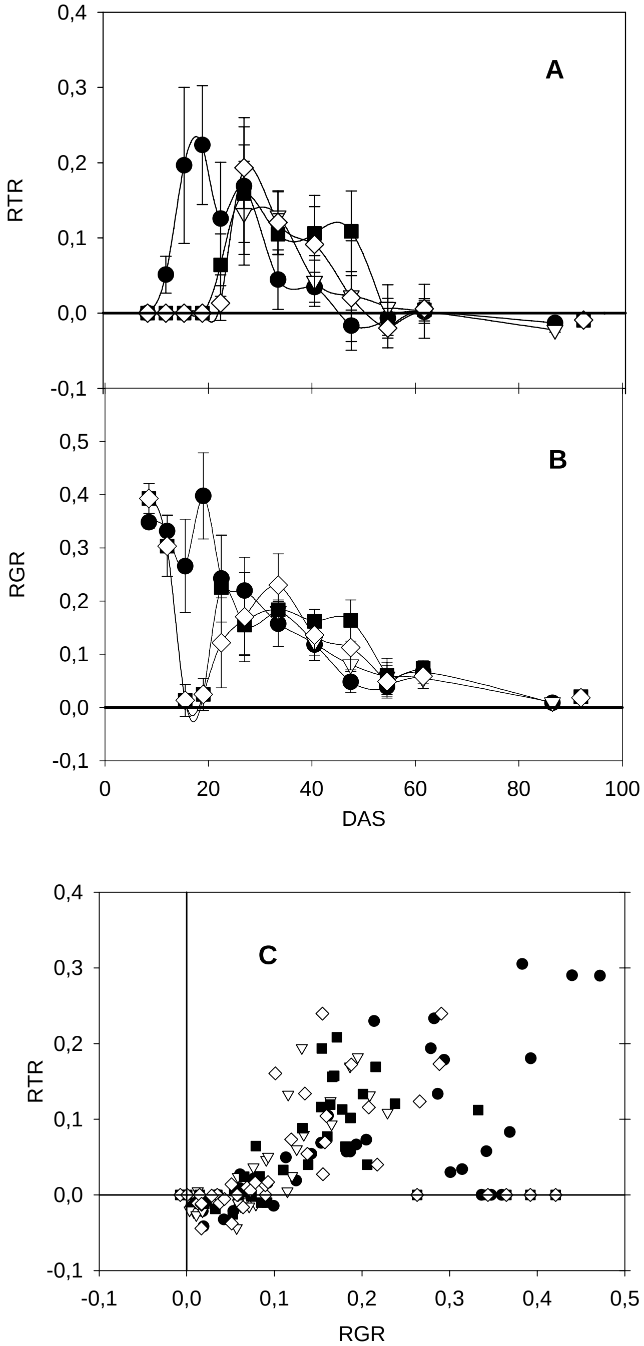


Fig. 19. Relative tillering rate (RTR) and relative growth rate (RGR) of all the four treatments (1=closed circles, 2=open downward pointing triangles, 3=closed squares, 4=open diamonds). **A.** RTR function of time, **B.** RGR function on time, **C:** RTR function on RGR. Points in A and B were the mean of the repetitions in each treatment, points in C were the values for each repetition in all the treatments.
RGR= ((DW2/DW1)^(1/(DAS2-DAS1)))-1 and was assigned to the date equal to the mean of DAS2 and DAS1. For RTR, dry weight (DW) was replaced by number of tillers.

RTR had quite the same behaviour along the growth period in all the treatments (**Fig. 19A**). After a rapid increase after transplanting until a maximum, it decreased to become negative. Plants did not synthesize tillers when they were still in the nursery, as a result, the rapid increase in RTR began later in the treatments WB 21. Nevertheless, RTR did not achieve the same value at maximum in WB 21 as in WB 07-25-NR. RTR might be higher afterwards in WB 21. The negative values of RTR occurred during tiller abortion. The same behaviour was also observed between treatments for RGR except for WB 21 during the nursery period (**Fig. 19B.**). RGR was the highest as soon as the plants were sowing. Then it decreased until 0 at the end of the growing period. A drop in RGR was noticed for the plants remained late (21 DAS) in the nursery. RGR increased again after plants were transplanted. No differences between treatments occurred thereafter. RGR and RTR were more or less linked by a linear relationship (**Fig. 19C.**). The interception on X was about 0.06. After this value of RGR, RTR increased as RGR increased in the same way in all treatments. Two groups of points were not on the linear relationship. The first one was characterized by a high RGR (0.25-0.45) and a RTR null or lower than 0.1 : it was related to the nursery stage. The second one was characterized by a high RTR but a RGR lower than the one which would have been read on the straight. It only consisted of points of WB 21 and WB 07-25-TR. For WB 21, it had to be related to the re-increase of RGR after it had become null during the nursery stage.

3- DISCUSSION

3.1. Observations on plants transplanted at 7 DAS at 25 plants m^{-2}

In this study, tillers appeared in the same order as the leaves on the main stem : primary tiller T3 emerged before T4 that emerged before T5… It was observed by Boone *et al.* (1990) and Skinner and Nelson (1994) that tiller emergence was driven first by tiller site formation at the base of every leaf associated with the regular leaf production and secondly by the number of buds that developed into tillers. Models have been elaborated to express the increase in number of tillers per plant. For example, in wheat and barley, tiller site formation has been relate to leaf appearance on the main culm by a Fibonacci series to determine potential tiller emergence in spaced plants (Kirby *et al.*, 1985; Boone *et al.*, 1990). But this approach implied a linear relationship between tiller sites and leaf appearance on the main tiller and an identical rate of leaf appearance for each axis at any time (Masle-Meynard and Sébillotte, 1981; Klepper *et al.*, 1982; Kirby, 1995). Increase in total number of tillers was first exponential, then became linear that suggested that, before maximum tillering, there was a regulation in the number of tillers appearing.

In this experiment, a high number of tillers per plant was produced (about 30 in WB 07-25-NR) but a great proportion was unproductive: 50 % of the tillers synthesized in treatment 1 did not produce grains at harvest. In the following parts, unproductive tillers will be called senescent tillers. T. Lafarge *et al.* (2002) showed that grain yield was highest when senescence of tillers was avoided or reduced, as for uniculm sorghum grown at 16 plants m-2, and tillering sorghum grown at four and eight plants m-2. This indicates that some of the resources captured by senescent tillers were probably wasted, even if senescent tillers may contribute to grain yield via translocation, as observed in barley during early stem elongation (Lauer and Simmons, 1988). Branch tillers which were also the most numerous at maximum tillering were the most senescent ones : primary tillers were only about 7 and senescent at less than 20 % unlike branch tillers which were about 20 and senescent at 60 %. They were also the most later formed and the lightest ones. The later formed tillers had the greater senescence percentage : primary tillers T9, T10 and T11 were senescent at more than 60 % and tillers in the colony of T6, T7, T8 and T9 at more than 80 %. They appeared later but they had the same maturity date and growth rate as the early formed ones , they were so the smallest ones. Ong (1978) noticed in grasses that the smallest or youngest tillers, irrespective of tiller position, tended to die first when the whole plant was stressed : these tillers had no more than 2 leaves each and no roots, hence they were completely dependent on the roots of the parent tiller for their water and nutrient supply. Senescence has to be related to general concepts associated with interplant competition and resource capture and senescent tillers could be defined as the less vigourous ones.

The same hierarchy between each individual colony was observed for frequency of each primary tiller, number of branch tillers, percentage of unproductive tillers and number of productive tillers at harvest, as it had been observed previously by Lafarge *et al.* (2002).The first tillers formed (T3,T4 and T5) had the greater number of tillers per colony and were also the most productive (higher number of filled grains) : productivity per individual primary tillers depended on the number of tillers produced since percentage of filled grains and average dry weight of filled grains did not vary significantly between each colony. Lafarge *et al.* (2002) suggested that fertility of individual tillers was driven by conditions at tiller emergence, via effects of tiller growth and development, as reported by Masle-Meynard and sébillotte (1981*b*). Green leaf area per tiller decreased with tiller origin in the same hierarchy to that for tiller emergence and fertility rate (Lafarge *et al.*, 2002; Lauer and Simmons, 1985): young tillers imported their assimilates preferentially from the subtending leaf on the main culm and from the leaf immediately above it. Similarly, Peterson *et al.* (1982) noticed that tiller emergence in wheat was highly reduced if its subtending leaf or the one above it was excised. Observations of low tiller emergence from the lower leaf axils compared with upper leaf axils have been reported by Lafarge (2002), Downes (1968), Masle-Meynard and Sébillotte (1981*a*) and Ong (1984) for sorghum, wheat and millet respectively. This effect in our experiment was slightly visible : not more productive tillers were present in colony 3 as in colony 4. Hence, the rate of emergence and subsequent fertility and yield of tillers from lower axils were probably affected by the small area of the subtending leaves that led to low tiller leaf area development., as already suggested by Cannell (1969*b*). Number of leaves of the tiller decreased as primary tiller number increased. Height and dry weight were nevertheless similar for main and primary tillers 3, 4 and 5. We can suppose that, thanks to a high disponiblility of assimilates at the time of their emergence through a high leaf area of their subtending leaf, the first primary tillers formed could catch the delay in growth they had with main or primary tillers of higher number.

3.2. The effects of the four treatments on plant's growth and productivity

Each treatment had the same productivity following a completely different tillering dynamic per plant:

(1) Tiller removal engendered a delay in tillering dynamic (about 4 to 5 days) without affecting the timing of the phenological stages and crop duration. Senescence rate was higher and number of productive tillers lower.

(2) Transplanting plants at 21 DAS engendered a delay in tillering dynamic two times greater than tiller removal and in the timing of the phenological stages, and increased crop duration. Contrary to tiller removal effect, main tiller and primary tiller's growth was delayed. Senescence rate was lower and number of productive tillers similar.

(3) To increase density from 25 to 50 plants m-2 engendered a tillering dynamic that stopped 3-4 days earlier. Senescence rate did not change and number of productive tillers was double.

Hence rice plants were able to adjust to various early crop management through their plasticity.

Removal of the first primary tillers resulted in a lower dry weight per plant and a higher senescence percentage, a lower yield would be so expected. Productivity was in fact not affected thanks to a lower phyllochron (time between the appearance of two successive leaves on a tiller) after 50 DAS and an over production of high order tillers. Leaf appearance rate of each primary tiller effectively decreased in the treatment where the first primary tillers had not been removed and tillers in each primary tiller colony stopped being synthesized. Indeed, plants which had already a lot of tillers at 45 DAS (maximum tillering) had to stop tillering not to be in shortage of assimilates afterwards. We can also notice that competition between tillers and search for light could have made the plants grow bigger in this treatment. Plants where the first primary tillers had been removed would not suffer from competition so early and primary tillers were present in a lower range at harvest but T5 and T6 had more tillers in their colony. Percentage of filled grains was also higher for each primary tiller. Plants invested effectively in this treatment more assimilates in the grains than in the stems as it was showed by a higher harvest index whereas total dry weight per plant was lower. In WB 07-25-NR, before maximum tillering, dry weight might have been attributed preferentially to the stems and tillers would have to stop being synthesized. As a result, the low number of productive tillers at harvest was compensated and productivity was the same as in WB 07-25-NR.

To transplant seedlings at 21 DAS instead of 7 DAS resulted in a delay in plant's growth dynamic. During nursery stage, competition between plants growing did not allow them to synthesize tillers. This absence of tillering was associated with a decrease in leaf appearance rate from 10 DAS until the transplanting date. Then, number of leaves increased and tiller emergence started. This delay in leaf appearance in WB 21 probably caused the delay in tiller emergence since leaf appearance and tiller appearance are related as it was suggested by Davies and Thomas (1983). Nursery management rather than transplanting shock, appear to be the reason for this delay. Schnier *et al.* (1990) proved that transplanting shock actually existed, but they did not check what was happening in the nursery. Delaying plant's age at transplanting resulted in a tillering reduced as it was observed by Dingkuhn *et al.* (1987) and a lower percentage of senescent tillers. The lower percentage of senescent tillers in the colony 3 and 4 actually compensated the lower number of tillers at maximum tillering. In WB 07-25-NR, those two tillers were the biggest ones and competition might have been the concept responsible for this higher senescence. Thanks also to a delay in maturity date, number of tillers were similar between both treatments at harvest. Harvest index was quite the same and, as a result, productivity was not affected. In a general way, less resources have been wasted in WB 21-25-NR and a longer interception of the light thanks to a longer crop duration compensated the lower number of tillers synthesized and resulted in the same productivity. As it was showed by the effect of tiller removal, plants adjusted to different conditions thanks to the first tillers that had appeared (T5 and T6 for tiller removal and T3 and T4 for late transplanting).

Plants transplanted at a density of 50 plants m^{-2} had the same growth dynamic as in WB 21-25-NR : tiller emergence was similar, the timing of the phenological stages did not change and maturity occurred at the same time. Fischer and Wilson (1975) observed also the same date of panicle initiation for sorghum despite varying the plant density from 1.5 to 65 plants m-2. The earlier occurrence of maximum tillering in WB 21-50-NR resulted in two times less tillers per plant but a similar number of tillers m^{-2}. Plants did not have the time to synthesize a lot of branch tillers, nevertheless they maintained the same average dry weight per tiller type all over the growing period : the emergence of small tillers was compensated by a gain in weight of the tillers already existing. Plants were able to adjust to two different density through a tillering regulation and to obtain the same productivity. In most cereals, grain yield is very stable over a wide range of plant densities as the tillering dynamics of the plant respond to the level of resources available (Seetharama *et al.*, 1984). Indeed, Darwinkel (1978) observed only a three-fold variation in grain yield in wheat associated with a 160-fold variation in plant density. This highlights the capacity of the plant to adapt its development to the amount of resources available, leading to a large range of tillering responses.

3.3. Modelling approach of tillering dynamic

The treatments induced a great variability in plant's growth through different tillering dynamics. Nevertheless relationships between parameters which were stable across the 4 treatments were established.

Thus, in all treatments, primary tillers n emerged at the time leaf n+3 appeared on the main tiller. In 1965, Friend already proposed that there was a constant "leaf interval" between the emergence of a leaf and the emergence of the tiller of its axil. In tall fescue, Skinner and Nelson (1994) also showed that leaves and tillers were associated : a high Leaf Elongation

Rate (low tillering) reduced maximum number of tillers to a greater extent than the low LER population by increasing leaf phyllochron sooner. Lafarge *et al.* (2002) in sorghum found that the dynamics of potentially fertile tillers number per plant varied greatly with plant density but tiller emergence rate aligned with leaf ligule appearance rate. These observations suggested that each potential tiller had the capacity to emerge and to grow for only a limited period. Similar qualitative results have been reported by Kirby and Faris (1972), Porter (1985) and Rickman *et al.* (1985), who found that each tiller on wheat had only one phyllochron during which it had the opportunity to initiate its development.

Maximum tillering occurred at a same value of LAI for each treatment between 2 and 2.5. Nevertheless no conclusion could be given for WB 07-25-TR. Maximum tillering was not the result of a given number of tillers since maximum number of tillers was slightly lower in WB 21-25-NR and WB 07-25-TR. Zhong *et al.*, (2002), conducted a study suggesting that LAI and N status were two major factors that influenced tiller production in rice crops. The objectives of this study were to quantify the critical leaf area index (LAIc) at which tillering stopped, and to determine the effect of nitrogen (N) on LAIc in irrigated rice. They found that tillering stopped at LAI of 3.36 to 4.11 when N was not limiting. Under N limited conditions LAI reduced to as low as 0.98. Transplanting spacing and number of seedlings per hill had little effect on LAIc, as we observed when density had been increased and as it had been noticed by Lafarge *et al.* (2002). The response of tiller emergence from LAI could be explained by the sensitivity of rice to neighbouring plants via variation in light quality. Ballaré *et al.* (1987) observed a reduced red : far-red ratio at low solar elevation for LAI values close to 1. This reduction was synchronous with a reduction in tiller production (Casal *et al.*, 1986; Gautier *et al.*, 1995). There was no clear relationship between cessation of tiller emergence and stem elongation (Lafarge *et al.*, 2002) contrary to the hypothesis of Ong (1984), for millet and Kirby *et al.* (1985) and Boone *et al.* (1990) for wheat. In fact, stem elongation is also known to be promoted by an decrease in the red : far-red ratio (Ballaré *et al.*, 1989; Kasperbauer and Karlen, 1994) and so both enhanced of stem elongation and reduced branching have been reported to be consequences of decrease in the red : far-red ratio (Ballaré and Casal, 2000).

RTR and RGR were related not by a so good relationship that the one exposed by Schnier *et al.* (1990) and Sugiyama (1995) in rice and tall fescue respectively. Nevertheless, we observed that tillering cessation was associated with a threshold RGR (6 % d-1) below which senescence starts as it was noticed by Dingkuhn *et al.*(1991). They hypothesized that the initiation of new tillers required the availability of a certain quantity of assimilates beyond the assimilates “committed” to growth of the organs already in place. This value proved to be stable for different varieties, sowing methods and levels of water limitation, but differed with growth stage and was only valid during the vegetative phase since additional sinks became active afterwards (Schnier *et al.*, 1990). The increase in RTR with the increase in RGR could be explained by the fact that growth through LAI and canopy architecture could determine photosynthesis and so tillering. Schnier *et al.* (1990) also assumed that growth, or assimilation, drove tillering, whereas tillering was not a major driving force for growth. The studies on light quality have indicated that cessation of tiller emergence is probably not the result of reduced assimilate availability in the plant. Deregibus *et al.* (1985) and Ballaré *et al.* (1987) observed that a decrease in tiller emergence occured prior to any appreciable shading and depletion of assimilate resources. Tiller (or stolon) production was reported to be reduced by a change in light quality for forage species, ryegrass, tall fescue, wheat, white clover and barley (Deregibus *et al*, 1985; Casal *et al.*, 1986; Kasperbauer and Karlen, 1986; Robin *et al.*, 1992; Davis and Simmons, 1994). The relationship between light quality and tiller emergence was confirmed when Casal *et al.* (1986) observed that an artificial increase in far-red light inhibited production of axes in clover. It is likely that changes in light quality, as an early signal of the presence of neighbours, allowed the plant to avoid wasting assimilate in tillers that would be unlikely to survive and become fertile (Skinner and Simmons, 1993). In fact, because green leaves absorb most of the red and reflect most of the far-red light, the ratio of red:far-red light decreases as density increases (Kasperbauer, 1987). An architectural plant or canopy variable could account for the light quality mediated effect of plant competition on cessation of tiller emergence.

CONCLUSION

To remove the first primary tillers appearing T2, T3 and T4, to delay plant's age at transplanting and to increase density at transplanting from 25 to 50 plants m-2 resulted in a similar productivity thanks to the plasticity of the plants expressed by different tillering dynamics. Plants were able to adjust to different early crop managements : is it worth trying to increase yield by early crop management ? Nevertheless, a lot of parameters might be inproved. Thus, plants transplanted at 7 DAS at a density of 25 plants m-2 still have a very high percentage of unproductive tillers next to 50 %, harvest index could be better as we observed for plants where primary tillers 2, 3 and 4 had been removed. In the dry season, yield tended also to be greater compared to the wet season (5.2 t/ha) and it was more obvious for plants transplanted at 7 DAS than for plants transplanted at 21 DAS (6.99 and 6.06 t/ha respectively). Maximum number of tillers was related to the percentage of unproductive tillers: to reduce maximum tillering thanks to genetic (by acting on LAIc for example) or crop management (as water or nitrogen stress) might be a good way to improve productivity.

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